

Differential control of the scapulothoracic muscles in humans

C. Alexander^{1,2}, R. Miley², S. Stynes^{2,3} and P. J. Harrison²

¹Department of Physiotherapy, Hammersmith Hospitals NHS Trust, Fulham Palace Road, London W6 8RF, UK

²Department of Physiology, University College London, Gower Street, London WC1E 6BT, UK

³School of Health Sciences and Social Care, Brunel University, Uxbridge, Middlesex UB8 3PH, UK

The control of the scapulothoracic muscles trapezius (Tr) and serratus anterior (SA) has been examined in normal human subjects. Electromyographic recordings were made from the SA and Tr muscles (upper trapezius UTr, lower trapezius LTr) using surface electrodes placed bilaterally. Magnetic stimulation of the motor cortex and electrical stimulation of peripheral nerves were used to examine their descending and reflex control. The average optimal site of cortical stimulation was found to be the same for SA, UTr and LTr (an approximate centre of gravity of -0.6 cm, 3.7 cm where the centre of gravity is expressed as the mean antero-posterior position, the mean medio-lateral position). Some asymmetry in the cortical representation of UTr was found in each individual tested. Magnetic stimulation evoked bilateral MEPs in Tr (latency contralateral (c) UTr 8.5 ± 1.6 ms, ipsilateral (i) UTr 19.0 ± 2.7 ms) but only contralateral responses were evoked in SA (11.2 ± 2.6 ms). Electrical stimulation of the long thoracic nerve at two sites was used to examine homonymous and heteronymous reflexes of SA, while electrical stimulation of cervical nerve of C3/4 was used to examine the heteronymous reflexes of Tr. Ipsilateral SA H reflexes were evoked at a latency of 9.9 ± 0.8 ms (proximal site) and 10.8 ± 1.2 ms (distal site). No group I reflexes were evoked from SA to its contralateral homologue. No group I reflexes were evoked between Tr and SA. Finally, cross-correlation of activity from the Tr muscle pairs and the SA muscle pair revealed that the motoneurons of the Tr muscles share some common presynaptic input whereas there was no detectable common presynaptic input to the SA muscle pair. This study extends and consolidates knowledge regarding the neural control of trapezius and for the first time explores the neural control of SA. The study demonstrates a contrasting bilateral control of Tr and SA. These patterns of connections are discussed in relation to the contrasting bilateral functional roles of these muscles.

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Corresponding author C. M. Alexander: Department of Physiotherapy, Hammersmith Hospital NHS Trust, Fulham Palace Rd, London W6 8RF, UK. Email: c.alexander@ucl.ac.uk

The trapezius and serratus anterior muscles are situated bilaterally upon the thoracic cage. When these muscles work together on one side, they stabilize and move the scapula enabling both stability and movement of the arm (Peat, 1986; Bernhardt *et al.* 1999). These muscles also act together to varying degrees with their contralateral counterparts during various activities. For example, when moving an arm, the activity of trapezius on the contralateral side can increase substantially (Smith *et al.* 2004). By contrast, only a small increase in the activity in the contralateral serratus anterior is observed (Smith *et al.* 2004). This contrasting behaviour of these two muscles contralaterally is surprising given that these muscles may have very similar functions when working together on one side.

In terms of the neural mechanisms controlling these muscles there is a paucity of information. There have been a variety of studies describing the behaviour of these muscles during movement, posture and a variety of tasks, both in normal individuals and in patients (Jensen & Westgaard, 1997; Westgaard & De Luca, 2001; Mork & Westgaard, 2006). However, there have been relatively few studies looking more directly at the neuronal pathways controlling them. The more extensive work relates to the descending control of trapezius. Gandevia & Applegate (1988) were the first to investigate a possible cortico-spinal projection to trapezius by electrically stimulating the scalp overlying the motor cortex. They observed, as expected, a short latency contralateral excitation of trapezius and also observed no effect on the ipsilateral

muscle. These observations were confirmed by Berardelli *et al.* (1991) using magnetic stimulation. However, more recently Bawa *et al.* (2004) investigated the bilateral control of a number of proximally and distally placed arm muscles including trapezius. However, unlike the two previous studies, Bawa *et al.* described an ipsilateral projection to trapezius in addition to the contralateral projection. This may or may not fit with expectations given progress in understanding the control of the axial musculature (see Discussion for further details). However, this discrepancy certainly warrants further investigation and was one of the issues that prompted the current study. In addition, there is no information available regarding the descending control of serratus anterior.

In terms of reflex connections, there is some limited information with regard to the control mechanisms of these muscles. In relation to trapezius, the trapezius muscle pair seems to be closely controlled by homonymous monosynaptic reflexes that cross the midline to the contralateral muscle (Alexander & Harrison, 2002). In relation to serratus anterior, there are no reports describing either the reflex control or the descending control of this muscle in humans. It is clear that serratus anterior is innervated by the long thoracic nerve, a nerve that exclusively supplies serratus anterior and which is described as being purely motor (Schultz & Leonard, 1992; Bizzarri *et al.* 2001). Given that this is the sole innervation, this is at odds with the observation that the muscle contains a normal complement of sensory receptors including muscle spindles (Voss, 1971). The long thoracic nerve is long and superficial and therefore is highly accessible to electrophysiological studies. Despite this, to our knowledge there have been no previous investigations of the reflex actions evoked by electrical stimulation of the long thoracic nerve. The present study takes advantage of the accessibility of this nerve in order to investigate the reflex connections of this muscle.

It is evident therefore that while the trapezius and serratus anterior muscles share the common function of securing the scapula to the chest wall, these two muscles also exhibit contrasting control. The present study aims to examine the neural basis of the differential control of these two large scapulothoracic muscles.

Methods

The experiments were approved by the ethical committee of University College London and conformed to the *Declaration of Helsinki*. Data were collected from a core group of 47 healthy subjects aged between 21 and 50 years from whom informed consent was obtained.

EMG recordings

Subjects were seated and surface EMG was recorded using rectangular adhesive electrodes (Blue Sensor disposable

electrodes; 4 mm by 7 mm in size) placed 3 cm apart. Recordings were made from two pairs of muscles at a time, a pair being taken to mean a particular muscle on one side of the body and its counterpart on the other side of the body. These pairs were either the serratus anterior muscle pair, the upper trapezius muscle pair or the lower trapezius muscle pair (see Alexander & Harrison, 2003 for details of electrode placement). The EMG was amplified (Digitimer NL824; Digitimer Ltd, Welwyn Garden City, UK) and filtered (Neurolog NL125; Digitimer Ltd) with a bandwidth of 30 Hz to 3 KHz. The data was converted from an analog to a digital signal at a sampling frequency of 4KHz (CED 1401; Cambridge Electronic Design, Cambridge, UK) and stored for later analysis by CED Signal software.

Location of areas of cortex controlling trapezius and serratus anterior

The appropriate sites of stimulation of the motor cortex for these muscles have not been previously documented. It was therefore necessary to systematically stimulate the scalp at different locations in order to create a map of effective foci for the different muscles. To achieve this a grid, drawn on a piece of cloth, was positioned on the head and centred around the mid-line and at the junction of the binauricular line using 16 subjects. A 90 mm figure-of-eight coil from the magnetic stimulator (Magstim 200; The Magstim Co., Whitland, Wales, UK) was held in place whilst 10 stimuli were delivered with the coil orientated 45 deg from the anterior posterior line. Different positions were explored while stimuli were applied in order to establish the position that evoked a MEP with the greatest amplitude. When this point had been established, the stimulator output was set to 1.2 times resting threshold for the MEP. The cortex was then stimulated at this and surrounding sites by positioning the coil systematically over the grid surrounding this optimal site.

The centre of gravity (COG) for each subject was calculated (see Boroojerdi *et al.* 1999 for details) and an average site for the COG was expressed as the mean coordinate \pm standard deviation. A two-way ANOVA without replication was used to assess whether the COG for each of the muscles recorded could be separated. So that a map of the motor cortex could be more easily visualized and compared between subjects, the MEP amplitude at 1.2 T at each grid position was expressed as a percentage of the optimal MEP amplitude for each subject. In 10 of the subjects, in order to examine the symmetry of the optimal area to evoke a MEP, the same methods were used on both sides of the scalp to map upper trapezius bilaterally.

In order to investigate how the responses to magnetic stimulation varied with stimulator strength and EMG activity, the cortex was stimulated at the optimal site at different stimulus intensities both at rest and in bilateral shoulder flexion at approximately 70 deg in the sagittal

plane (14 subjects). The stimulus intensities used generally ranged from 20% to 100% of the stimulator's output and recruitment curves were subsequently constructed for any responses. The threshold for any response was expressed as the percentage of the stimulator output. The latency of any contralateral response at $1.2 \times$ motor threshold at the optimal site of stimulation was recorded. As repeated recordings were taken from a number of the subjects, an average latency for each individual was used to calculate the final average latency \pm standard deviation. The EMG was also rectified and averaged in order to better visualize any inhibitions and the ipsilateral response. The latency of any ipsilateral response was also recorded. It was rarely possible to measure the latency at $1.2 \times$ the threshold for the ipsilateral response as these responses were evoked at high stimulus outputs. The latency was taken at the first clear deflection from baseline activity.

Reflex activity evoked by electrical stimulation of the nerve to serratus anterior

Activation of the afferent fibres of serratus anterior was achieved by electrical stimulation of the long thoracic nerve. The cathode, a roving gauze covered probe was used to locate the long thoracic nerve. This nerve can be located superficially at two points (i) proximally, superior to the proximal end of the clavicle (7 subjects, Williams *et al.* 1989) and (ii) distally, on the lateral surface of the chest wall along the mid-axillary line (7 subjects). Confirmation that the cathode was located on the long thoracic nerve was ascertained by the resulting contraction of the serratus anterior muscle. As the nerves to serratus anterior and trapezius are closely situated in this supra clavicular fossa, it was also ensured that no M response in trapezius occurred during these recordings. The anode, a gauze covered metal plate, was positioned just below the clavicle. EMG recordings were collected whilst the subject was at rest as detailed above. A series of 10 stimuli were delivered for each average. The EMG was averaged and the latency of the resulting reflex was measured.

Reflex activity evoked by electrical stimulation of the afferent nerve to trapezius

Activation of the afferent fibres of trapezius was achieved by electrical stimulation of the cervical nerve of C3/4, which is superficially located on the anterior surface of the upper fibres of trapezius above the clavicle (see Alexander & Harrison, 2002). The cathode, a roving, gauze covered probe was used to locate the nerve and was deemed to be satisfactorily located when no serratus anterior M response was evoked alongside the trapezius reflex. In addition, the activity of infraspinatus was monitored since its nerve supply, the suprascapular nerve, is also closely situated. When the nerve was satisfactorily located the cathode

was replaced with a self-adhesive Ag–AgCl electrode. The anode was positioned below the clavicle. The cervical nerve of C3/4 was stimulated at an interstimulus interval of 3 s. EMG recordings were collected whilst the subject was at rest as detailed above. In two (of the five) subjects, the procedure was repeated on a number of separate occasions. The EMG activity was averaged and the latency of the resulting reflex was measured. As the procedure was repeated with some subjects, each subject's mean latency was used to construct the final results.

Cross-correlation of EMG from trapezius and serratus anterior

In order to perform a cross-correlation analysis of the EMG of different muscles, recordings were made (in six subjects) from different muscles taken two at a time. The combinations studied were the left and right lower trapezius, the left and right upper trapezius and the left and right serratus anterior. Subjects were asked to maintain a weak contraction of these muscle pairs by flexing the arms to approximately 90 deg in the sagittal plane. This was aided by visual and auditory feedback of the EMG signal. Surface, multiunit EMG recordings were collected as detailed above and stored on the PC using CED Spike software. Large amplitude spikes from multiple units (approximately 3700) were selected from the EMG of both muscles using level detectors (Neurolog NL200). These trigger pulses were also converted to a digital signal (CED 1401) and stored on the PC using Spike software. Cross correlograms were constructed from the spikes using a 1 ms bin width and a recording period of 100 ms before and after the triggered period.

The size of any peak within the correlogram was measured in terms of peak bin count divided by the mean bin count (κ). To ensure an accurate reflection of the mean, the mean bin count was measured away from any central feature. A peak was significant if it was more than two standard deviations above the mean bin count. The standard deviation was calculated as the square root of the product of the number of extra spikes above the mean and the interspike interval (Davey *et al.* 1986). Any differences in the size of the peak between the muscle pairs were analysed using a two-factor analysis of variance without replication.

Results

Magnetic stimulation of the scalp overlying the motor cortex at the optimal site (see below) evoked MEPs in the contralateral muscles of upper and lower trapezius and in serratus anterior in 16 subjects (Fig. 1A). At rest, the latency at 1.2 MT of the contralateral MEPs for upper trapezius was 10.4 ± 1.1 ms (threshold of $53.2 \pm 8.2\%$), for lower trapezius was 12.3 ± 1.4 ms ($56.9 \pm 7.0\%$) and

for serratus anterior was 12.0 ± 1.1 ms ($58.0 \pm 4.8\%$). With a weak contraction, the latency at 1.2 MT decreased to 8.5 ± 1.6 ms ($42.5 \pm 13.6\%$) for contralateral upper trapezius, 11.2 ± 1.8 ms ($36.7 \pm 7.5\%$) for lower trapezius and 11.2 ± 2.6 ms ($38.8 \pm 12.2\%$) for serratus anterior. In addition, a contralateral inhibitory response was also evoked infrequently. At rest the latency at 1.2 MT of the contralateral inhibitions for upper trapezius was 41.8 ms (threshold of 55%; 17% occurrence), for lower trapezius was 39.5 ± 3.8 ms ($55 \pm 0\%$; 33% occurrence) and for serratus anterior was 47.1 ± 0.3 ms ($55 \pm 0\%$; 33% occurrence).

At rest, facilitatory responses were also recorded ipsilaterally in the upper and lower trapezius muscles, albeit at higher stimulus strength. However, they were only recorded in three subjects out of 11 tested at rest. These responses were of a longer latency than the corresponding contralateral response (upper fibres of trapezius 30.4 ± 1.5 ms, lower fibres of trapezius 33.8 ± 15.4 ms). During a weak contraction an upper trapezius ipsilateral response was evoked more frequently (11 subjects out of 13 tested) at a latency of 19.0 ± 2.7 ms, i.e. longer than the corresponding contralateral response. In addition, an ipsilateral long latency inhibition was evoked in nine subjects out of the 13 tested at a latency of 50.4 ± 12.1 ms. In contrast no ipsilateral serratus anterior

responses were evoked even at high stimulator outputs or with ongoing muscle activity (Fig. 1B).

Location of effective sites on the scalp to evoke MEPs in trapezius and serratus anterior

Using a roving coil, the scalp was systematically stimulated to evaluate the most appropriate site of stimulation for evoking MEPs in contralateral serratus anterior and trapezius muscles in 10 subjects. The amplitude of the MEP was expressed as a percentage of the amplitude of the largest response. Typical maps for three subjects are illustrated in Fig. 2A. The COG for each muscle has been expressed as the mean antero-posterior position \pm s.d., the mean medio-lateral position \pm s.d. The serratus anterior COG was -0.6 ± 0.8 cm, 3.8 ± 0.5 cm, the COG for upper trapezius was -0.5 ± 0.9 cm, 3.7 ± 0.7 cm and finally the COG for lower trapezius was -0.7 ± 0.7 cm, 3.7 ± 0.6 cm. The locations of the optimal sites for different subjects are illustrated in Fig. 2B. Figure 2B also shows the close correspondence of the average COG of upper and lower trapezius and serratus anterior. These COGs cannot be statistically or indeed experimentally separated in either the antero-posterior direction ($P = 0.94$) or medio-lateral direction ($P = 0.30$).

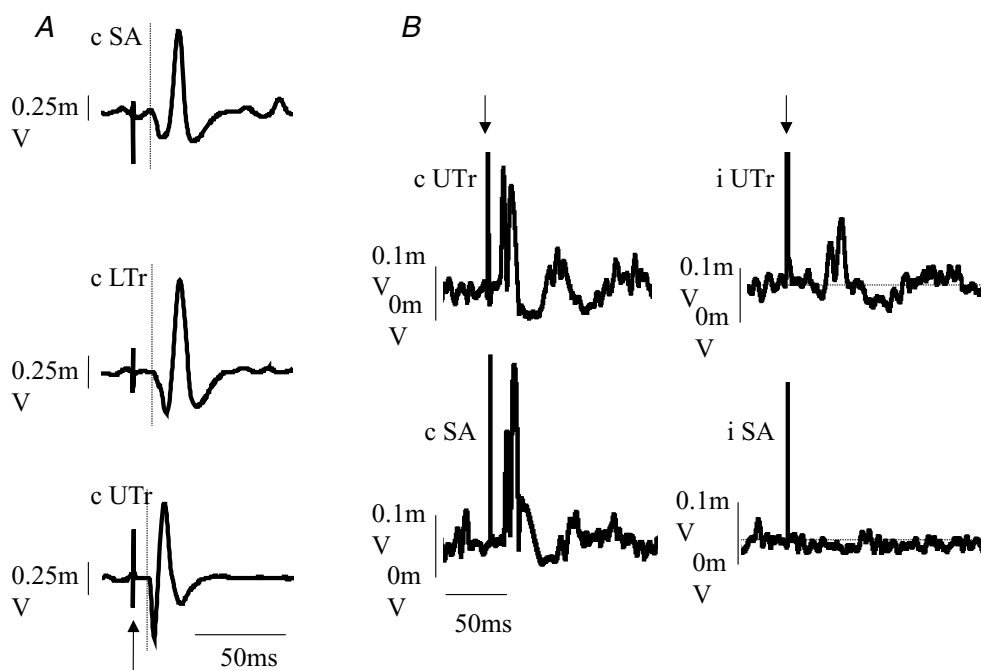
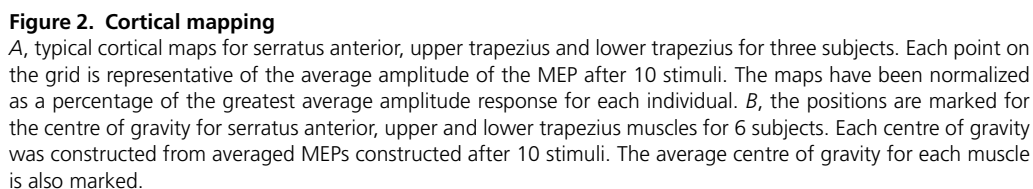


Figure 1. MEPs evoked in serratus anterior and trapezius

A, average contralateral MEPs from serratus anterior (upper trace), lower trapezius (middle trace) and upper trapezius (lower trace). These MEPs are the average of 10 sweeps. The artifact is marked with the arrow. The vertical dotted line marks the onset of the MEP. B, averaged rectified MEPs of upper trapezius (top) and serratus anterior (bottom). The contralateral response is on the left with the ipsilateral response on the right. These MEPs are the average of 20 sweeps. The arrows mark the stimulus artifact.



In 10 individuals maps were constructed on both the left and the right scalp (while recording from the contralateral upper trapezius). Interestingly, the site of the optimal position to evoke a trapezius MEP for each individual tended to be asymmetrical when right and left normalized maps were viewed (Fig. 3). That is, in 9 of 10 subjects maps were asymmetrical in either the antero-posterior direction by at least 1.5 cm or the medio-lateral direction by at least 1.5 cm (see Fig. 3). However, when the left and right optimal site co-ordinates and COGs were compared these differences were not significant in the pooled data (e.g. anterior/posterior average COG difference 0.87 ± 1.02 and medial/lateral average COG difference 1.49 ± 1.31 ; $P = 0.16$).

Reflex activity evoked by electrical stimulation of the afferent nerve to trapezius

As described in our previous studies (Alexander & Harrison, 2002), electrical stimulation of the afferent nerve

to trapezius evoked a monosynaptic response in trapezius bilaterally (latency of these reflexes are 10.9 ± 1.4 ms ipsilaterally and 11.9 ± 1.5 ms contralaterally). In these experiments this has been confirmed and extended to investigate any reflex effects on serratus anterior. No reflex connection from trapezius to serratus anterior could be evoked either ipsilaterally or contralaterally (five subjects tested).

Reflex activity evoked by electrical stimulation of the long thoracic nerve

Electrical stimulation of the long thoracic nerve evoked an H reflex in serratus anterior at short latency. This could be evoked from stimulation of the long thoracic nerve at both the proximal and distal sites stimulated. When stimulating at the proximal site, the H reflex latency was $9.9 \text{ ms} \pm 0.8 \text{ ms}$ (7 subjects). Here, the M response could be seen in every subject ($4.0 \pm 0.8 \text{ ms}$; see Fig. 4). When

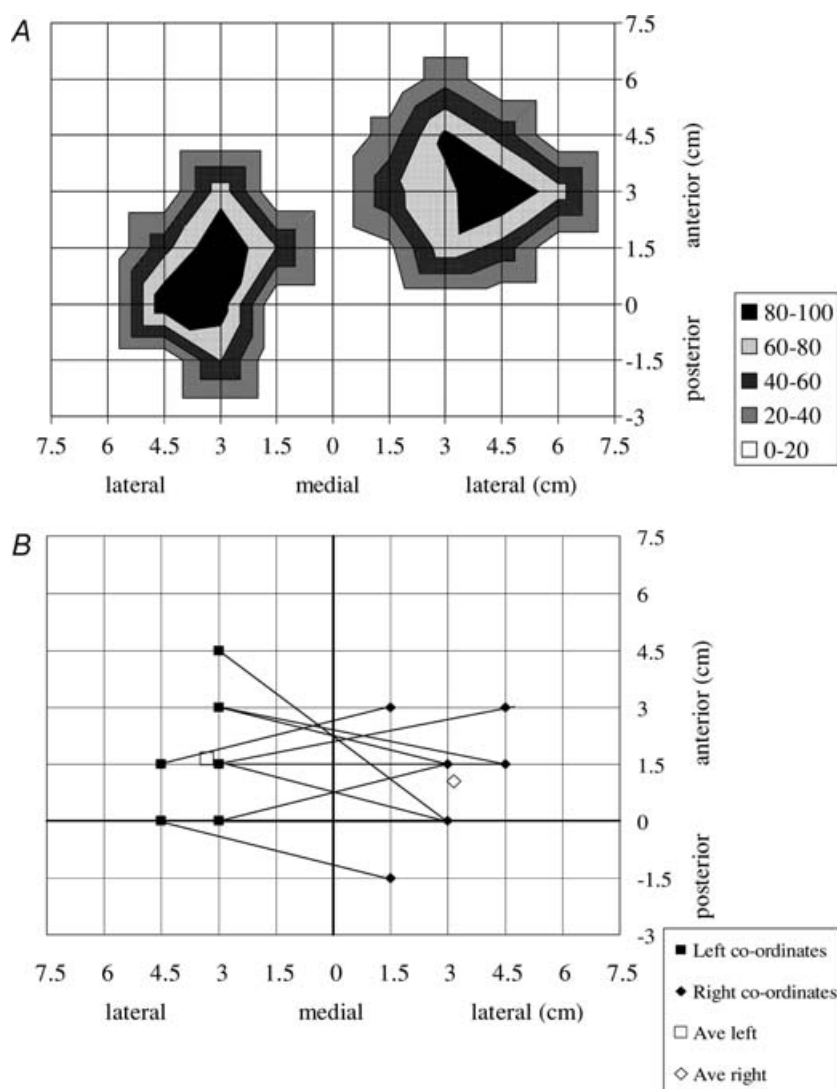


Figure 3. Asymmetry of cortical map for contralateral upper trapezius MEPs

A illustrates a cortical map for contralateral upper trapezius MEPs evoked from the left and right hemispheres from one individual. The asymmetry of the map is also illustrated by the population results, B. Here the position of the largest amplitude average contralateral MEP for each individual is marked. It is linked by a line to that evoked from the opposite side.

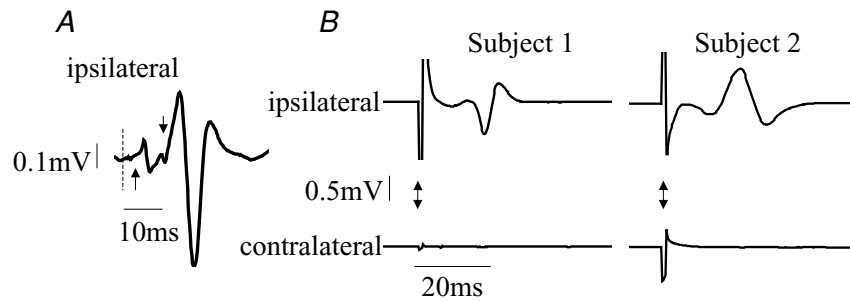


Figure 4. Serratus anterior H reflexes

A, typical example of the ipsilateral serratus anterior H reflex evoked from the proximal site of stimulation. This reflex is the average of 10 sweeps. The vertical dashed line marks the stimulus onset. The upward pointing arrow marks the onset of the M response, and the downward pointing arrow marks the onset of the H reflex. B, two examples of the average ipsilateral serratus anterior H reflex evoked from the distal site (top). No contralateral response is seen (bottom). The stimulus artifacts are marked by the arrows. The responses are an average of 10 sweeps.

stimulating at the distal site, this reflex was evoked at a latency of 10.8 ± 1.2 ms (7 subjects). Because of the proximity of the stimulation site to the serratus anterior muscle, an M response could not always be distinguished since it often occurred during the decay phase of the stimulus artifact.

Electrical stimulation of the long thoracic nerve never evoked a short latency reflex in contralateral serratus anterior muscle (7 subjects at the proximal site and 7 subjects at the distal site; see Fig. 4). This stimulation also never evoked a short latency reflex in trapezius ($n = 14$; see Fig. 5).

Cross correlation of EMG from trapezius and serratus anterior

As we have previously described, significant short duration peaks are seen in the cross-correlograms constructed between multiunit spike trains between the upper and lower trapezius muscle pairs and between upper and lower trapezius muscles ipsilaterally (Alexander & Harrison, 2002). The present work extends these observations to include combinations with serratus anterior. Examples of the various combinations are shown in Fig. 6. The most striking finding in this further study is the lack of short duration peak in the correlogram between serratus anterior and its contralateral homologue (no detectable short duration peak in 6 subjects tested). This is in contrast to the significant short duration peaks in the correlograms for both the left and right upper trapezius muscle pair (strength of correlogram (k) is 1.9 ± 0.7 ; present in 6 of 7 subjects tested), and the left and right lower trapezius muscle pair ($k = 2.4 \pm 0.9$; present in 7 of 7 subjects tested).

Discussion

Using three different approaches the results of this study describe both contrasts and similarities in the neural control of serratus anterior and trapezius.

The cortical control of the scapulothoracic muscles

Using magnetic stimulation of the motor cortex, contralateral MEPs could be evoked in all serratus anterior and trapezius muscles tested. In trapezius, this is to be expected and is in accordance with the studies of Gandevia & Applegate (1988), Berardelli *et al.* (1991), Truffert *et al.* (2000) and Bawa *et al.* (2004). The latency of the contralateral upper trapezius MEPs is consistent with that found by Berardelli *et al.* (1991) and Truffert *et al.* (2000) and indeed the early evoked responses are compatible with fast corticospinal projections to the motoneurone pools.

In addition to a contralateral response, magnetic stimulation also evoked ipsilateral responses in trapezius. The latency of this response was 10.5 ms longer than that evoked contralaterally. This latency difference suggests that the ipsilateral response is unlikely to reflect a direct ipsilateral corticospinal projection. Such bilateral MEPs in trapezius have recently been described by Bawa *et al.*

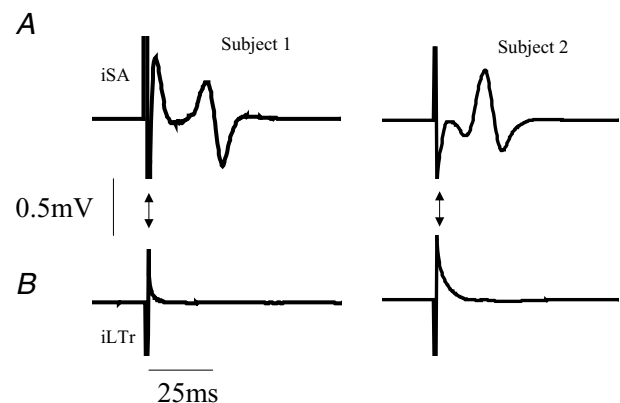


Figure 5. Selective action of serratus anterior afferents

A, two examples of the average ipsilateral serratus anterior H reflex evoked from the distal site. B, no ipsilateral trapezius response is seen. The stimulus artifacts are marked by the arrows. The responses are an average of 10 sweeps.

(2004). In this work recordings were made from a number of upper limb muscles and the incidence of ipsilateral responses compared between muscles. They reported that ipsilateral responses are more frequently evoked in the more proximal muscles by comparison to forearm and hand muscles. Similar results were reported by Strutton *et al.* (2004) who noted a higher incidence of evoking ipsilateral MEPs in the proximal abdominal muscle, internal oblique, by comparison to the low incidence observed in arm and hand muscles. Such a relationship is also supported by the bilateral MEPs recorded in the diaphragm, rectus abdominis and masseter muscles by Carr *et al.* (1994). However, this distal to proximal trend does not seem to hold true for the scapulothoracic muscles in the present study – no ipsilateral MEPs could be evoked in serratus anterior in contrast to the clear responses in trapezius. This leads us to search for alternative hypotheses to account for our observations. One obvious possibility is that bilateral control might reflect the bilateral functionality of particular muscles rather than their anatomical position. Indeed, certain muscles such as masseter and the diaphragm have obvious bilateral functionality. Some trunk muscles (e.g. rectus abdominis and internal oblique) work bilaterally during arm and leg movements as well as movement of the spine (Peach *et al.* 1998; Hodges *et al.* 1999). Trapezius works bilaterally during upper limb and neck movements (Smith *et al.* 2004). On the other hand, the serratus anterior muscle pair does not work together to the same degree during movement of the arm when compared to these other proximal muscles (Smith *et al.* 2004). Specifically, protraction of the scapula, to which serratus anterior is a prime mover, is clearly a movement of one arm and largely independent of movement of the other arm. What therefore seems to be important in determining whether a muscle is bilaterally controlled from the cortex is not the

proximal–distal location of the muscle, but on the bilateral functionality of the particular muscle.

In studying the bilateral descending control of these muscles using TMS, it was necessary to search for the optimal site of stimulation on both sides of the scalp. When the COGs for the contralateral MEPs evoked in upper trapezius from either the left or right motor cortex were compared across the subjects, there was no asymmetry found. A similar result has been reported by MacKinnon *et al.* (2004) in relation to two other shoulder muscles, latissimus dorsi and pectoralis major. However, when we examined our individual data, it became apparent that the optimal site of stimulation was often 1.5 cm different when comparing the two sides. This may not be functionally significant. It may reflect slight variations in location of the precentral gyrus within the skull or it may reflect imperfections in our stimulating technique. What is important, however, is that in experiments of this kind when comparing the responses evoked from one side with those evoked from the other it should not be presumed that the optimal site of stimulation on the scalp is symmetrical.

Finally, with the techniques employed, the COGs for trapezius and serratus anterior are indistinguishable. This may be because either they share a common area of the motor cortex or the resolution of the technique is not sufficiently high to discriminate between the different cortical areas.

The reflex control of the scapulothoracic muscles

The contrasts in bilateral control of trapezius and serratus anterior using magnetic stimulation of the motor cortex are mirrored in our observations on the reflex control of these muscles. A new approach adopted in this study is to investigate the reflex actions of afferents in serratus

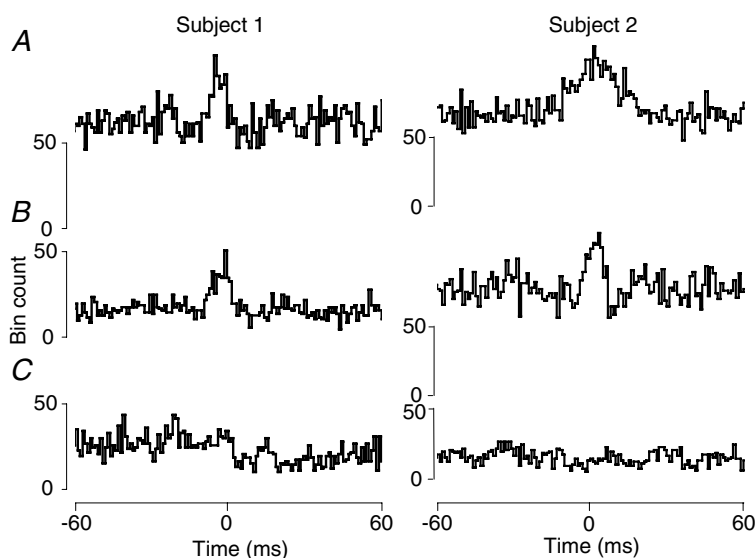


Figure 6. Cross-correlation of the trapezius and serratus anterior muscles

The cross-correlograms were constructed from two subjects during abduction of the arms between multiunit spike trains generated from the bilateral upper fibres of trapezius (A), the bilateral lower fibres of trapezius (B), and the bilateral serratus anterior muscles (C).

anterior by stimulating the long thoracic nerve either in the supraclavicular fossa or along the lateral chest wall. The result of stimulating this nerve is to evoke an H reflex in serratus anterior homonymously. However, of greater interest is the observation that stimulation of this nerve evoked no reflex in the contralateral serratus anterior. This is in contrast to stimulating the nerve to trapezius, which evokes a clear H reflex in the contralateral trapezius (Alexander & Harrison, 2002).

In relation to ipsilateral synergistic reflexes between serratus anterior and trapezius, no reflexes were evoked from serratus anterior to trapezius, neither were reflexes evoked from trapezius to serratus anterior. This is in contrast to other synergistic muscles within the arm for which one can evoke monosynaptic group I facilitatory reflexes (Baldiessa *et al.* 1981; Cavallari & Katz, 1989; Schomburg, 1990; Cavallari *et al.* 1992). Thus, it is surprising that reflexes were not recorded between serratus anterior and trapezius even though they work synergistically to stabilize and move the scapula during use of the arm. However, further light on this issue is cast by the study in the cat by Caicoya *et al.* (1999). They explored the pattern of group I projections between a number of muscles in the shoulder and forelimb and described how synergistic groups of muscles share bi-directional monosynaptic group I projections. However, unlike these functionally synergistic groups, the few group I reflexes from serratus anterior that they were able to characterize revealed a relatively isolated pattern of connections that were unidirectional from serratus anterior to supraspinatus and triceps. This is therefore in accordance with our observations in humans that serratus anterior also has a rather isolated pattern of connections. In addition to Cacoia, Fritz *et al.* (1989) described patterns of synergistic unidirectional, bidirectional and skewed group I monosynaptic connections in the forelimb of the cat. Both these studies suggest that patterns of bi-directional synergistic reflexes serve to co-ordinate movement about joints which have one degree of freedom. In addition, they also suggested that joints with more complex kinematics, where muscles sometimes work synergistically but are also required to work in an uncoupled fashion, do not have such direct reflex projection. This might be the case for trapezius and serratus anterior as, although these muscles work together to produce rotation of the scapula and to maintain a stable scapula during movement of the hand and arm, they also work separately to produce movements such as elevation, depression and protraction of the scapula.

Differential control of scapulothoracic muscles revealed using cross-correlation analysis

Cross-correlation of the electromyographic activity has become an established procedure for identifying common

last order inputs to different groups of motoneurons (e.g. Carr *et al.* 1994; Gibbs *et al.* 1995; Keen & Fuglevand, 2004). The approach cannot easily be used to identify which inputs to motoneurons are common; rather the approach identifies which groups of motoneurons have significant shared presynaptic input. The rationale for using this approach in these experiments was that if serratus and trapezius are indeed under different degrees of bilateral control then this ought to be reflected in the cross-correlograms of these pairs of muscle bilaterally. Indeed, as previously described (Alexander & Harrison, 2002), a significant degree of correlation is observed between the respective heads of trapezius on either side of the body. Presumably, this represents, at least partly, the common input from group I afferents since they monosynaptically activate contralateral, as well as ipsilateral, trapezius motoneurons (Alexander & Harrison, 2002). By contrast, no significant peak occurred when correlating the activity of the serratus anterior muscle pair suggesting no significant last order presynaptic input project to serratus motoneurons bilaterally. This contrast reinforces the view that the two serratus anterior muscles have very limited, if any, common last order input, not only from a lack of group Ia inputs, or bilateral descending inputs but also from other prospective common inputs such as those from common interneurons.

Summary

In summary, trapezius and serratus anterior are two bilateral, proximally placed muscles located upon the trunk. The trapezius muscle pair are closely controlled having a bilateral cortical connection and crossed monosynaptic reflexes. However, the serratus anterior muscle pair are controlled independently of each other without the same bilateral cortical control and without crossed monosynaptic reflexes. This difference in control gives insight as to the common and separate functions of these two proximal muscles. A key issue is the attachments of trapezius to the spine. This allows bilateral action of trapezius to produce extension of the cervical spine. In addition, trapezius on one side may function to counter balance the action of trapezius on the opposite side in order to maintain the position of the spine, whilst acting to lift one arm. However serratus anterior, without the spinal attachments functions unilaterally during arm movements. There is less requirement to co-ordinate a bilateral contraction with its contralateral muscle pair. Thus, even though they are both proximally positioned, differences are revealed when comparing their bilateral control with their contralateral counterpart. These results suggest that the mechanisms of control of muscles across the body are not due to their proximal to distal position but are due to their bilateral function.

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